

6-21-2011

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### Recommended Citation

Rotman, Amy (2005) "The Robust Australopithecines: Evidence for the genus *Paranthropus*," *Totem: The University of Western Ontario Journal of Anthropology*: Vol. 13: Iss. 1, Article 11.

Available at: <http://ir.lib.uwo.ca/totem/vol13/iss1/11>

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# The Robust Australopithecines: Evidence for the genus *Paranthropus*

## Keywords

robust australopithecines, *Paranthropus*, morphological, trait analysis

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with the fossil KNM-WT 17000 as the initial specimen through whom the *Paranthropines* evolved. Through a trait analysis, a paradigm analysis, and an ecological and taxonomic discussion I will be able to better interpret the fossil record of the robust australopithecines. Through the examination of the concepts of traits, paradigm, and ecology and taxonomy, it will be argued that the differences between the robust australopithecines and the gracile australopithecines is great enough to warrant the use of the genus name *Paranthropus* in dealing with the robust species, specifying that they are in fact a separate clade from the Australopithecines and later *Homo*.

### Trait Analysis

The chronology of early hominid phylogeny is wrought with differing interpretations as to the exact sequence of human evolution. Of great concern is the determination of which species is considered the last common ancestor of the *Paranthropus* lineage and of the *Homo* lineage, if we do concede to the generic splitting of the two forms. The position taken in this paper is that the *Paranthropus* and *Homo* clades diverged approximately 3-2.5 million years (MY) ago from a common ancestor of *Australopithecus afarensis* (Chamberlain 1991:141).

A trait analysis is required in order to gain an understanding of general morphological differences and similarities among the early hominids. Broadly speaking, the cranial and dental traits of the *Paranthropines* suggest specializations that relate to heavy chewing—most likely of coarse, tough, fibrous plant foods (Foley 1995:84). The earliest evidence of the divergence into the *Paranthropine* lineage was marked by the appearance of the fossil KNM-WT 17000, otherwise known as the “Black Skull.” Found in deposits in West Turkana, Kenya, KNM-WT 17000 (from here on named *Paranthropus aethiopicus*), was initially assigned to the species *Paranthropus boisei*, based on several of its robust features, such as the extremely large size of the palate and the teeth (namely the molars and premolars), the build of the infraorbital and nasal areas, and its dish-shaped midface with forwardly positioned zygomatic bones (Klein 1999:213). It will later be demonstrated that this initial taxonomic naming is misleading, and therefore the taxonomic name *Paranthropus aethiopicus* is used for this specimen. It is widely acknowledged that amongst the robust group of

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Of great debate among anthropologists over the past few decades is the identity of the “robust” australopithecines and if this group warrants a separate genus name, *Paranthropus*, to distinguish them from the “gracile” australopithecines. The first robust australopithecine to be discovered was found by Robert Broom in 1949 in South Africa and was named *Paranthropus robustus*. Since then however, debate has raged on concerning the validity of the species name *Paranthropus*. A variety of models have been presented to account for various interpretations of the fossil materials of the robust australopithecines. This paper will focus on two polar extreme views of taxonomy: one that consolidates all hominid species into a single lineage, and another that allows for the splitting of hominid branches into two distinct genera. A critical examination will be undertaken in this paper, dealing specifically

early hominids, robusticity of traits increased through chronological history. Therefore, it is noted that *Paranthropus robustus* and *Paranthropus boisei* were markedly more robust than the earlier *Australopithecines* in many of their features. Whether these two specimens were simply geographic variants of one another or they reflected a greater taxonomic distinction is currently under debate. However, these contemporaneous species did share an extraordinary number of characteristics. It is in their masticatory apparatus where the description 'robust' applies. While their incisors and canines were relatively small, their cheek teeth were greatly expanded -- as noted in the fact that their deciduous and permanent premolars were almost fully molarized (Klein 1999:215). As compared to the more gracile australopithecines, whose teeth do not show such extreme changes in size, the robusts' teeth are said to be indicative of a more specialized dietary adaptation.

In terms of skull morphology, the robust group of early hominids is in direct contrast with both the earlier, gracile australopithecines, as well as with the larger-brained early hominids, beginning with *Homo habilis*, who existed contemporaneously with them. The robust species' dish-shaped faces were characterized by very powerfully built zygomatic arches which arise far forward on the maxilla (Klein 1999:215). Their mandibles were very thick and deep, with tall and broad ascending rami which arise much more laterally and inferiorly than those found in *Australopithecus afarensis* (Klein 1999:215). These traits, along with their anteriorly placed sagittal crests, reflect a much greater emphasis on the temporalis muscle and other bones, which suggests an increased specialization in mastication. *Homo* specimens are seen to be lacking in the dental specializations noted in the paranthropines, as they have much smaller and more parabolic jaws. They have more even sized (generalized) teeth and much longer and larger brain cases which stand at around 600-700 cc (Foley 1995:84). In addition to this, *Homo* faces are small and much less prognathous than those found in the paranthropines (Foley 1995:84).

When Walker initially assigned KNM-WT 17000 to *Paranthropus boisei*, the forty features used to show their close affinity actually provide us with misleading interpretations. In a more recent analysis of the same material conducted by Kimbel, White and Johanson (1988), it was shown that sixteen of the forty character states that were displayed by KNM-

WT 17000 (that were previously believed to specifically tie it to *Paranthropus boisei*) were actually chronologically primitive traits that are shared with the last common ancestor, *Australopithecus afarensis*. As well, thirteen out of sixteen derived characteristics that were common between KNM-WT 17000 and *Paranthropus boisei* were revealed to be present in other Australopithecine fossils (Kimbel *et al.* 1988:260). Based on these re-analyses, Kimbel *et al.* (1988) show that there were only three characters used in Walker's analysis which directly link KNM-WT 17000 with *Paranthropus boisei*. With this in mind, I can argue that the fossil KNM-WT 17000 is morphologically dissimilar to *Paranthropus boisei* and therefore, it must be understood as a separate species, one that was intermediate between the early australopithecines and the later, more robust paranthropines. Kimbel *et al.*'s (1988) re-analysis of the character traits of KNM-WT 17000 deals with thirty-two traits. Of these, twelve are primitive to *Australopithecus afarensis*, six are derived traits shown to be shared with all later hominids (including *Australopithecus africanus*, *Paranthropus robustus*, *Paranthropus boisei*, and to a small extent early *Homo*), an additional twelve were derived and shared with only the paranthropines, and only two were shown to be derived and shared exclusively with *Paranthropus boisei* (Kimbel *et al.* 1988:261).

In the above re-analysis, the characteristics analyzed demonstrated the affiliation of KNM-WT 17000 to the other early hominids. The primitive traits demonstrated KNM-WT 17000's derivation from the earlier *Australopithecus afarensis*. These features also ruled out *Australopithecus africanus* as the last common ancestor for the Paranthropines and the early Homos. The primitive characters shared by KNM-WT 17000 and *Australopithecus afarensis* were not demonstrated in the *Australopithecus africanus* fossils, therefore to include them at the beginning of the lineage of the Paranthropines would imply an extraordinary amount of character reversals. The remaining derived features shared in common with KNM-WT 17000 and the Paranthropines implies that they are all part of the same phylogeny, evolving from *Australopithecus afarensis* (in whom these features were not demonstrated). Those derived traits also exhibited in *Australopithecus africanus* are understood to be parallelisms.

A phylogenetic hypothesis to best demonstrate the affinity of these early hominids,

taking into account the suite of character traits previously discussed, is that *Australopithecus africanus* is the exclusive ancestor of *Homo*. There are a number of derived characteristics used to confirm the validity of this hypothesis, including an overall reduction in pneumatization of the mastoid process of the temporal bone, an increase in steepness of the frontal bone, and a mean increase in the relative length of the upper occipital (Kimbel *et al.* 1988:263). This hypothesis requires the least amount of parallelisms and is therefore the most parsimonious in examining early hominid phylogeny. Therefore, through the analysis of character traits performed by Kimbel *et al.* (1988), a clear tree of phylogenetic relationships can be drawn to demonstrate that KNM-WT 17000 (*Paranthropus aethiopicus*) and *Australopithecus africanus* diverged from *Australopithecus afarensis* several million years ago. The robust paranthropines evolved from the fossil KNM-WT 17000, while the early *homos* evolved from *Australopithecus africanus* in a separate branch of evolution.

#### Paradigm Analysis

In understanding the phylogenetic relationship that is accepted in this paper, it is important to be aware of how a particular paradigm can greatly affect one's analysis and interpretation of the fossil record. Phylogeny is concerned primarily with the course of evolution and the branching or diverging events which take place. Dating and morphology of the fossil record suggests that the hominid fossil record constituted a number of distinctive evolutionary branching events as opposed to comprising of a single evolutionary lineage (Foley 1995:72). The phylogeny of the hominid lineage that I propose is that between 3 and 2.5 MY ago, *Australopithecus afarensis* was the last common ancestor to lead to two diverged lineages, the megadontic specialists (the Paranthropines), and the larger-brained generalists (*Homo*). However, despite evidence that is continually debated amongst anthropologists, there is still no consensus as to which phylogenetic framework is the best representative of human evolution. This is the problem of paradigm.

Each anthropologist brings his or her own biases and worldviews into an analysis of the fossil record, and these are consequently reflected within the hypotheses, methodology, and conclusions at which they arrive. As Wolpoff (1976) discusses in a paper on the theory behind paleoanthropological

controversies, all data exists within a theoretical framework. Wolpoff explained that the field of paleoanthropology is almost subjective in the sense that "there are neither refutation nor proofs...only probability statements for which any and all observations are appropriate" (Wolpoff 1976:95). In this sense, Wolpoff conceded that the field of anthropology does rely upon differing paradigms and that each anthropologist's paradigm will bring a new interpretation on the old material.

A difference in opinions on trait list bias is shown in the papers written by Skelton and McHenry (1998) and in Strait and Grine (1998), which discussed early hominid phylogeny. Skelton and McHenry criticize Strait and Grine's grouping of *Paranthropus aethiopicus* with *Paranthropus robustus* and *boisei* to create a monophyletic clade. Skelton and McHenry's (1998:109) analysis placed *Paranthropus aethiopicus* within the sister clade of *P. africanus*, *P. robustus*, *P. boisei*, and *Homo*. These varied phylogenies were arrived at because of different assumptions and procedures which relate to the effect of trait list bias. The distinctions that are noted are due to different assumptions of correlations among traits, as well as an unequal representation of the functional complexes of traits (Skelton and McHenry 1998:109). Although this trait list bias is agreed upon as causing problems in both analyses, there is no consensus between these groups of anthropologists as to how to compensate for the bias.

Strait and Grine (1998:115) believe that the best chance for arriving at an agreement over early hominid phylogeny requires an open discussion about characteristics and methodology. They evaluate Skelton and McHenry's (1998) analysis, and in particular their use of functional groupings of traits. They explain that Skelton and McHenry's separation of the anterior dentition from the traits relating to heavy chewing does not qualify as a valid functional grouping. Diet is responsible for trends seen in both anterior and posterior dentition, as well as in other masticatory features of the skull, and therefore, anterior dentition cannot be separated from this grouping (Strait and Grine 1998:115). In this sense, we can see how each group's paradigm affects the ways in which they group character traits.

Strait and Grine (1998) believe in character trait lists that take into account characteristics that are not only functionally related, but also phylogenetically compatible

with one another -- this is the nature of cladistic theory. They state that Skelton and McHenry (1998) use complexes which are not reasonable within cladistics. The phylogenetic relationship accepted in this paper is in agreement with that of Strait and Grine (1998). *Paranthropus aethiopicus* is shown as being differentiated from *Australopithecus afarensis*, and early *Homo* through its megadontic characteristics. Anterior dentition morphology is directly related to heavy masticatory action and is thus considered part of a similar functional complex as the rest of the masticatory apparatus which functions to sustain heavy chewing.

### An Ecological and Taxonomic Discussion

Approximately 3-2.5 million years ago, conditions of cooling and drying arose on the African landscape; this was the first widespread North Polar glaciation. As Vrba (1988:407) explains, physical, environmental changes that have evolutionary repercussions can arise from two sources: tectonic plate movement which is relatively localized, and global climatic changes which are widespread. The global event which occurred 2.5 million years ago initiated both climatic and biotic changes within Africa. The result of these changing conditions was the creation of more extensive open habitats and a change in the form of vegetation to a more resistant arid-tolerant variety (Bromage and Schrenk 1995:110). The amount of woodland available decreased greatly, and early hominids were forced to adapt to living in an open savanna habitat. The selective pressures that arose in conjunction with the changing environmental landscape resulted in the phyletic splitting of *Australopithecus afarensis* into two separate lineages, *Paranthropus* and *Homo* (Bromage and Schrenk 1995:110).

Adaptations to the environment and to coarse, fibrous food items are noted in the first paranthropine, *Paranthropus aethiopicus*. Throughout time, the *Paranthropus* lineage adapted itself more fully to this new open habitat. As can be noted in the later Paranthropines, facial robusticity and megadonty prevailed throughout the existence of the genus. The robust lineage became more specialized in response to resources that were prevalent in these more open environments. Vrba proposes a functional link between the robust cranial morphology of the Paranthropines and the food resources that were prevalent within the open, arid environments that they occupied. Based on an analogy of the functional morphologies of

other mammals, Vrba (1988) explains that the robust dental and cranial morphology directly reflects an adaptation for feeding on tough foods. This is best seen in the robust cranial characteristics: greatly thickened tooth enamel, the expansion of cheek teeth (the molars and premolars) and a reduction of the anterior (canines and incisors) teeth, as well as pronounced and expanded areas of insertion for the immense masticatory muscles (Vrba 1988:418). Through an analysis of these traits, it seems clear that the robust features were an adaptation to the changing ecology of the environments occupied in Africa and the foods eaten by the paranthropines.

An examination of another early hominid species living contemporaneously with *Paranthropus*, *Homo habilis/ rudolfensis*, illustrates a parallel evolution in some of the features associated with this adaptation to a more open, savanna environment (Bromage and Schrenk 1995:110). Many of the masticatory and dental adaptations seen in the cranium of early *Homo* demonstrate a similar adaptation to tougher fruit and savanna foods. However, the *Homo* lineage is considered much more generalized in terms of its dental traits than the paranthropines. The evolutionary trajectory that *Homo* followed turned out to be very different from that of *Paranthropus*.

It can be argued that the key variable in the endurance and survival of the australopithecines and *Homo* was 'culture' and the paranthropines were lacking in this ability for culture. Although the environmental pressures resulted in extreme adaptations, the *Homo* lineage was able to further adapt to changing environments because of their use of 'culture' in terms of the development of more sophisticated tools. The environment provided these separate genera with a series of selective challenges to which they adapted through similar means. However, approximately 2 MY ago, the environment once again underwent great changes and returned to dryer and more humid conditions.

Fossil evidence suggests that *Paranthropus boisei* dispersed southward in Africa, and under these more moderate conditions, evolved into *Paranthropus robustus* (Bromage and Schrenk 1995:112). This is argued because fossil evidence suggests that *Paranthropus robustus* was a less extreme version of the "hyper-robust" *Paranthropus boisei*. It can be argued that while the early Paranthropines adapted to the cool, dry climate



and open savanna by developing more robust features in order to survive on the tough foods available, *Paranthropus robustus* existed in a much more temperate environment and thus a slight reversal in the robusticity of the skull developed.

This biogeographic perspective helps us to further understand the forces that acted upon the phylogenetic splitting of the early hominids into these two very distinct groups, with *Paranthropus aethiopicus* leading the way for the more megadont Paranthropines. I argue that ecological forces were the main pressures that acted in producing these separate lineages of early hominid evolution.

### Concluding Notes

A great problem plaguing modern anthropologists concerns the placement of the robust group of early hominids within the evolutionary line. Although many people argue for a single lineage for the evolution of the early hominids, it can be demonstrated that this is not necessarily a logical argument. When evaluating whether the robust group constitutes genetic-level differences from the Australopithecines and early *Homo*, one must take into account general morphological differences between fossils, the bias of paradigm and its influence on one's professional work, as well as ecological concerns.

In an analysis of the traits of the *Paranthropus* lineage in comparison to the Australopithecines and early *Homo*, it has been demonstrated that the primitive and derived traits allow for the genetic-level splitting of the Paranthropines, using *Australopithecus afarensis* as the last common ancestor. This was primarily visible in the Paranthropines' unique dental and cranial specializations that relate to mastication. In an examination of the issue of paradigm, it is noted that every individual brings his or her own biases and world-views into an experiment, and therefore, we must examine all sides of an argument and draw our own conclusions regarding their validity. In terms of ecological variables, it is demonstrated that changing environmental and climatic changes have a great influence on the adaptation and survival of early hominids. The shifting ecology of the Plio-Pleistocene required that the early hominids adapt to their new environments and habitats. The results of these adaptations were specializations so unique to the Paranthropines as to make a genetic-level split from the Australopithecines and *Homo* logical. Therefore,

as outlined in the previous arguments, there is sufficient evidence to argue for the genus *Paranthropus*, deriving from a last common ancestor of *Australopithecus afarensis*.

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